

# AMERICAN MUSEUM *Novitates*

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY  
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, N.Y. 10024  
Number 2895, pp. 1-18, figs. 1-15

November 4, 1987

## A Hypothesis on the Homology of Proboscidean Tusks Based on Paleontological Data

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### ABSTRACT

The nature and development of proboscidean tusks has long been discussed. New observations, mainly on the Upper Miocene elephantoid species *Amebelodon floridanus* (Leidy), and comparisons with other fossil proboscideans (*Moeritherium* and different elephantoid taxa) lead to the conclusion that the tusks of *Moeritherium* and of Elephantoidea are not homologous. Factors considered were the precocity of incisor development and succession in elephantoids, the observed associa-

tion of the two pairs of lower incisors protruding out of the symphysis for a short period of time, the position of the loci in the premaxilla and the mandibular rostrum, and the hypothesis of homology of the loci in *Moeritherium* and elephantoids. It is proposed that the two pairs of incisors of elephantoids are incisors of the first dentition with no dental replacement and the permanent incisors (tusks) are dI2/di1.

### RÉSUMÉ

La nature et le développement des défenses chez les proboscidiens ont depuis longtemps fait l'objet de controverses. De nouvelles observations, principalement chez l'éléphantoïde d'âge Miocène supérieur *Amebelodon floridanus* (Leidy), jointes aux comparaisons avec d'autres proboscidiens fossiles (*Moeritherium* et différents éléphantoïdes) mènent à la conclusion suivante: les défenses de *Moeritherium* et des Elephantoidea ne sont pas homologues. A partir de la précocité du développement et de la succession des incisives chez les éléphan-

toïdes, de l'association des deux paires d'incisives saillant hors de la symphyse pendant une courte période de temps, de la position des loci dans le prémaxillaire et le rostre de la mandibule, de l'hypothèse d'homologie des loci chez *Moeritherium* et les éléphantoïdes, les deux paires d'incisives des éléphantoïdes sont interprétées comme des incisives de première dentition sans remplacement, les incisives permanentes (défenses) seraient les dI2/di1.

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## INTRODUCTION

The interpretation of proboscidean tusks is still debated. The most common opinion is that a dental replacement occurs in elephants (Laursen and Beckoff, 1978: 2; Shoshani and Eisenberg, 1982: 2) and that (see for instance Sikes, 1971: 80) the elephant tusk I2 is preceded by dI2 (sometimes called the tush, the use of the term being then restricted to the transitory incisor [Sikes, 1971] and not to small incisors regardless of their number or homology). This interpretation follows Andrews' (1906) well known hypothesis of homology between the elephant tusk and the inflated I2 of the Paleogene genus *Moeritherium*, the latter being the sister group of both Deinotheriidae and Elephantoidea (fig. 1).

An alternative was Anthony's (1933: 117) hypothesis that in elephants both tusk and transitory incisor belong to the same dentition. For Anthony, the "incisive transitoire" is the second incisor, the "incisive définitive" (tusk) is the third, and both probably are deciduous incisors (Anthony, 1933: 120).

It should be noted that few fossil specimens are known which show tush and tusk associated. One example is a mandible of *Mammuth americanum* described by Peterson (1926); others are a mandible of *Platybelodon grangeri* described by Osborn and Granger (1932), a mandible of *Moeritherium lyonsi* described by Tassy (1981), and a skull of a tetralophodont gomphothere described by Tassy (1986). New material studied in this article belongs to the species *Amebelodon floridanus* (Leidy) from the Upper Miocene (Early Hemphillian) of Mixson's Bone Bed (Florida), and to *Gomphotherium angustidens* (Cuvier) and *Archaeobelodon filholi* (Frick) from the Middle Miocene (Astaracian) of the Aquitaine Basin (France). The various specimens allocated to *Amebelodon floridanus* include skulls and mandibles of different individual ages with incisors in situ and also isolated incisors.

The deinotheres are excluded from the discussion because (1) deinotheres had no upper incisors, (2) the sequence of tooth development of the lower incisors, which are inflated and form evergrowing tusks, is not known, though Stehlin (1925: 157, fig. 27) allocated

isolated small incisors called "milk incisors" to deinotheres.

## ACKNOWLEDGMENTS

I thank H. Shoshani for critically reviewing the manuscript and providing helpful comments.

The specimens of *Amebelodon floridanus* belong to the Frick Collection of the American Museum of Natural History in New York. I studied them in 1978 and 1985 courtesy of R. Tedford, M. C. McKenna, and M. Novacek. During my first visit to the AMNH, E. Manning offered me guidance in the Frick Collection. Financial support was given by the C.N.R.S. (R.C.P. 292, dir. Y. Coppens, and U.A. 720, dir. J.-J. Jaeger). Financial support for fieldwork in En Péjouan, Aquitaine Basin (France) was given by the C.N.R.S. (L.A. 12, former dir. J.-P. Lehman), the Muséum National d'Histoire Naturelle (Paris), and the Université Paris VI. Specimens from Sansan and Baigneaux (MNHN) were studied courtesy of L. Ginsburg; specimens from Castelnau-Barbarens and Crastes were studied courtesy of D. Vidalenc (Saint-Gaudens). The drawings were made by D. Visset.

## ABBREVIATIONS

AMNH	American Museum of Natural History, New York
CV	Collection Vidalenc, Saint-Gaudens
F:AM	Frick Collection, American Museum of Natural History, New York
MNHN	Muséum National d'Histoire Naturelle, Paris

## INCISOR DEVELOPMENT IN *MOERITHERIUM*

The dental formula of anterior teeth of *Moeritherium* is: 3I 1C/2I 0C, interpreted as I1 I2 I3 C/1 i2. The loss of the lateral lower incisor, i3, is usually assumed following Andrews (1906) because of the medial position of the two lower incisors, close to the symphyseal plane.

Part of the sequence of tooth replacement for *Moeritherium* had been described by Tas-

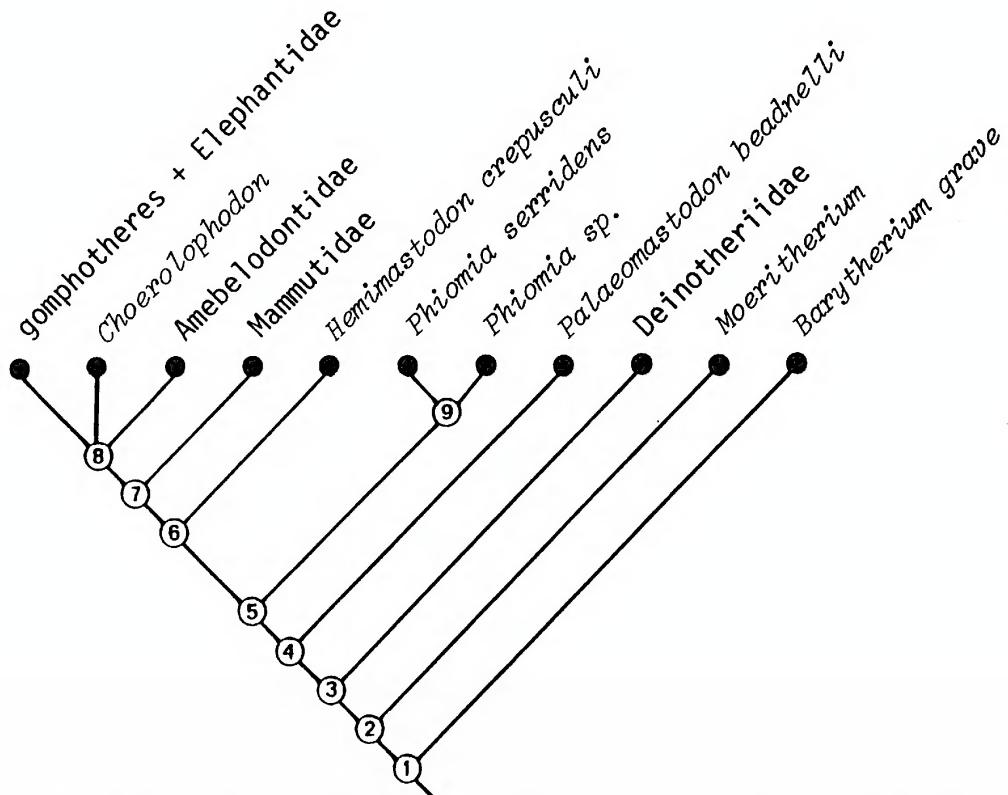


Fig. 1. Summarized interrelationships of the Proboscidea. The fourth dichotomy corresponds to what are called here elephantoids, the sixth dichotomy corresponds to the ancestral morphotype of known Neogene to Recent elephantoids (see Tassy, 1982, for detailed explanations).

sy (1981: 114, fig. 11), based on the observation of a complete mandible. This specimen shows erupted p3–m2 and erupting p2; the germ of m3, dissected, is still inside the dentary. Each half mandible shows one medial unworn incisor with lateral enamel buds at the tip, and a more lateral incisor, more gracile, which has an anterolateral wear facet. The lateral incisor is followed posteromedially by the germ of another incisor of greater size with lateral enamel buds at the tip. The interpretation is the following: the medial incisor is a permanent incisor (i1) which had been just erupted on this specimen (the enamel is unworn). The lateral incisor is a deciduous tooth (di2) in function, followed by its replacing tooth (i2). This interpretation follows Andrew's (1906) hypothesis of the loss of the lateral incisors (di3–i3). The replacement of a deciduous incisor by an in-

flated permanent incisor appears to be well established. Andrews (1906: 121, pl. 8, fig. 1-1A; pl. 9, fig. 11) already described a skull of a slightly older individual with P2M2 in situ, P2 being unworn and M3 erupting. The inflated incisor (tusk) is also erupting; and its late eruption, is coincident with that of M3. Its size matches the big incisors (I2) known on other adult skulls of *Moeritherium* (i.e., one already described by Andrews, 1906: pl. 10, fig. 3). This is in close agreement with the situation observed on the mandible. Of the loci of lower incisors of *Moeritherium*, Andrews knew only the alveoli: the biggest was the more lateral (i2). Schlosser (1911: pl. 16, fig. 6) subsequently described a small symphyseal fragment with two fresh incisors on each side, which can be interpreted as milk incisors (di1 and di2) because of their small size and thinness of the enamel layer. As for

the skull, this specimen is in agreement with the interpretation of the developmental succession described on the more mature mandible (Tassy, op. cit.).

The timing of the eruption of I<sub>2</sub> and i<sub>2</sub> is the same: it follows the eruption of P<sub>2</sub> and p<sub>2</sub> and just precedes (or is contemporaneous with) that of M<sub>3</sub> and m<sub>3</sub>. This correlation leads to the conclusion that in the genus *Moeritherium* the eruption of the tusks (I<sub>2</sub> and i<sub>2</sub>) is late. The tusks are not truly hypodont. Andrews (1906: 106) has already shown that, unlike the elephant tusk, the root is closed in adults.

#### INCISOR DEVELOPMENT IN THE ELEPHANTOIDEA

As already stated, living elephants have a pair of small upper incisors (transitory incisors) which precede the tusks, but no lower incisors. Nevertheless, the ancestral morphotype of the Elephantoidea had a pair of evergrowing lower tusks which can be observed in the African Oligocene species *Phiomia seridens* from the Fayum (Andrews, 1906) and in the primitive species of most Neogene elephantoid monophyletic groups, including Mammutidae (Tassy and Pickford, 1983), Amebelodontidae, and Elephantidae with their stem group—the gomphotheres (Frick, 1926, 1933; Osborn, 1936; Ginsburg and Antunes, 1966; Tassy, 1984, 1986). Moreover, primitive Elephantidae retained lower tusks (genera *Stegotetrabelodon* and *Primelephas*; see Maglio, 1973). The homology of the tusks of primitive elephantids and of various non-elephantid elephantoids is clear.

Though isolated incisors have been interpreted as milk incisors and allocated to "mastodonts" (see for instance Stehlin, 1925: 166, 176, figs. 28, 31; 1926: 693), the development of the incisors was not known in these studies. This sequence can be deduced from the study of rare specimens which show both incisors associated.

#### UPPER INCISORS

As in living elephants, the transitory incisors of fossil elephantoids are shed very rapidly so that specimens with both upper incisors in each premaxilla are rare. This association is known in two elephantoid taxa.

One belongs to the gomphotheres and the other to the Amebelodontidae. The gomphothere has been described by Tassy (1986: fig. 34) as a "tetralophodont gomphothere (gen. et sp. indet.)". It was discovered by Martin Pickford in the Upper Miocene Ngorrora Formation of the Baringo Basin (Kenya). The skull has a broken rostrum and shows two incisors on the left side. The more lateral is sectioned; one can see only the flat and unopened transverse section of the root (interpreted as the tush or "incisive transitoire"). The tip of the more medial incisor is untouched. The enamel cap has a ventral ridge. Compared to juvenile tusks of *Gomphotherium angustidens*, this tooth was interpreted as the "incisive définitive" (tusk) at an earlier stage of development than that of the more lateral transitory incisor.

The amebelodontid described in this article belongs to the species *Amebelodon floridanus* from the Early Hemphillian of Mixson (Florida), formerly allocated to the genus *Serridentinus* and later transferred to *Amebelodon* (see Turner, 1975). The Mixson's Bone Bed has yielded extraordinary material, including several skulls and mandibles of different individual ages in which the sequence of incisor development can be seen.

As for elephants, dental ages based on the eruption and wear pattern of jugal teeth had been proposed for the trilophodont species *Gomphotherium angustidens* (see Tassy, 1985: 285–308), which can be applied to every species with the same dental formula and grade; this is the case for *Amebelodon floridanus*. The complete sequence of incisor development can be seen from dental age I to dental age III, that is, during eruption and wear of DP<sub>2</sub> and DP<sub>3</sub> and eruption of DP<sub>4</sub>.

Crania of juvenile *Amebelodon floridanus* of dental ages I, II, and III show (1) the position in the premaxilla of both incisors, (2) the development of each incisor. Previously, only one of the two incisors (the permanent tusk) had been observed *in situ* in juvenile specimens of other fossil elephantoids like the European species *Gomphotherium angustidens* (see for instance Tassy et al., 1977: 219, figs. 5, 6).

Among the specimens of *Amebelodon floridanus*, a cranium of a newborn (F:AM 99402; fig. 2) with erupting DP<sub>2</sub> and DP<sub>3</sub> (dental

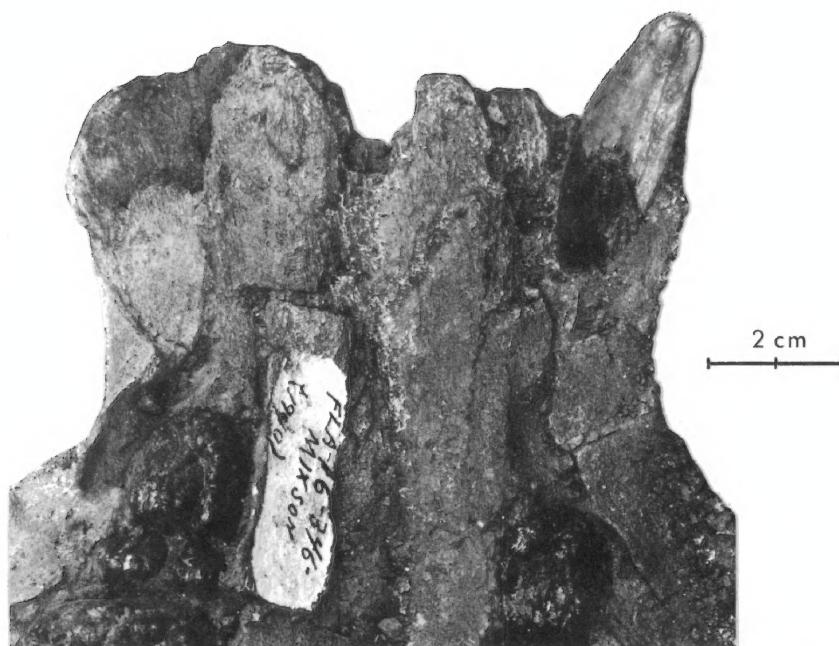


Fig. 2. *Amebelodon floridanus*, rostrum showing left dI3 (skull with erupting DP2–3, F:AM 99402). Mixson's Bone Bed (Early Hemphillian), Florida.

age I) shows on the left side one incisor in situ in the premaxilla, close to the sutural plane with the maxilla. This incisor barely protrudes out of the premaxilla. The tip of the incisor is recovered by an enamel cap with a ventrolateral ridge. A distinct cervix separates the enamel cap (crown) from the rest of the tooth composed of dentine recovered by a layer of cement (root), which is rather flat. The measurements for F:AM 99402 are: visible length of the lateral incisor (transitory incisor) on the ventral side 43 mm; length of the enamel cap 31 mm.

Another skull (F:AM 99415; fig. 3) shows the association of the two incisors on each side; its dental age is II (erupted DP2–DP3). The more lateral incisor protrudes out of the premaxilla. Its tip is recovered by an enamel cap with a ventrolateral ridge, as for the erupting incisor of F:AM 99402. The enamel is worn at the tip. The transverse section of the tooth is flattened mediolaterally. The other incisor is a tooth germ situated medially to the erupted incisor. It is entirely recovered by an enamel layer with a ventrolateral ridge. This germ has the same morphology as the germ described in *Gomphotherium angusti-*

*dens* by Tassy et al. (1977, op. cit.) as the permanent tusk. Measurements of F:AM 99415 are: visible length of the left lateral incisor (transitory incisor) 140 mm; length of the protruding part of the lateral incisor 60 mm; visible length of the left medial incisor (tusk) 40 mm; transverse section of the left medial incisor 21.3 × 6.0 mm.

The shedding of the lateral incisor can occur either during the dental ages II or III. One skull of *A. floridanus* (F:AM 99487), the dental age of which is III, shows only one incisor on each side protruding out of the premaxilla. At the tip the ventrolateral ridge of the enamel cap extends toward the origin; ventrally it forms the border of a lateral enamel band distinct from the cement layer which covers the rest of the tooth. This is the early stage of the development of the large enamel band seen on mature tusks. This tooth is the permanent tusk, which corresponds to a later stage growth of the medial incisor described on F:AM 99415. Measurements of F:AM 99487 are: visible length of the right incisor (tusk) 170 mm; length of the protruding part 110 mm.

Another skull of dental age II (F:AM 99454)

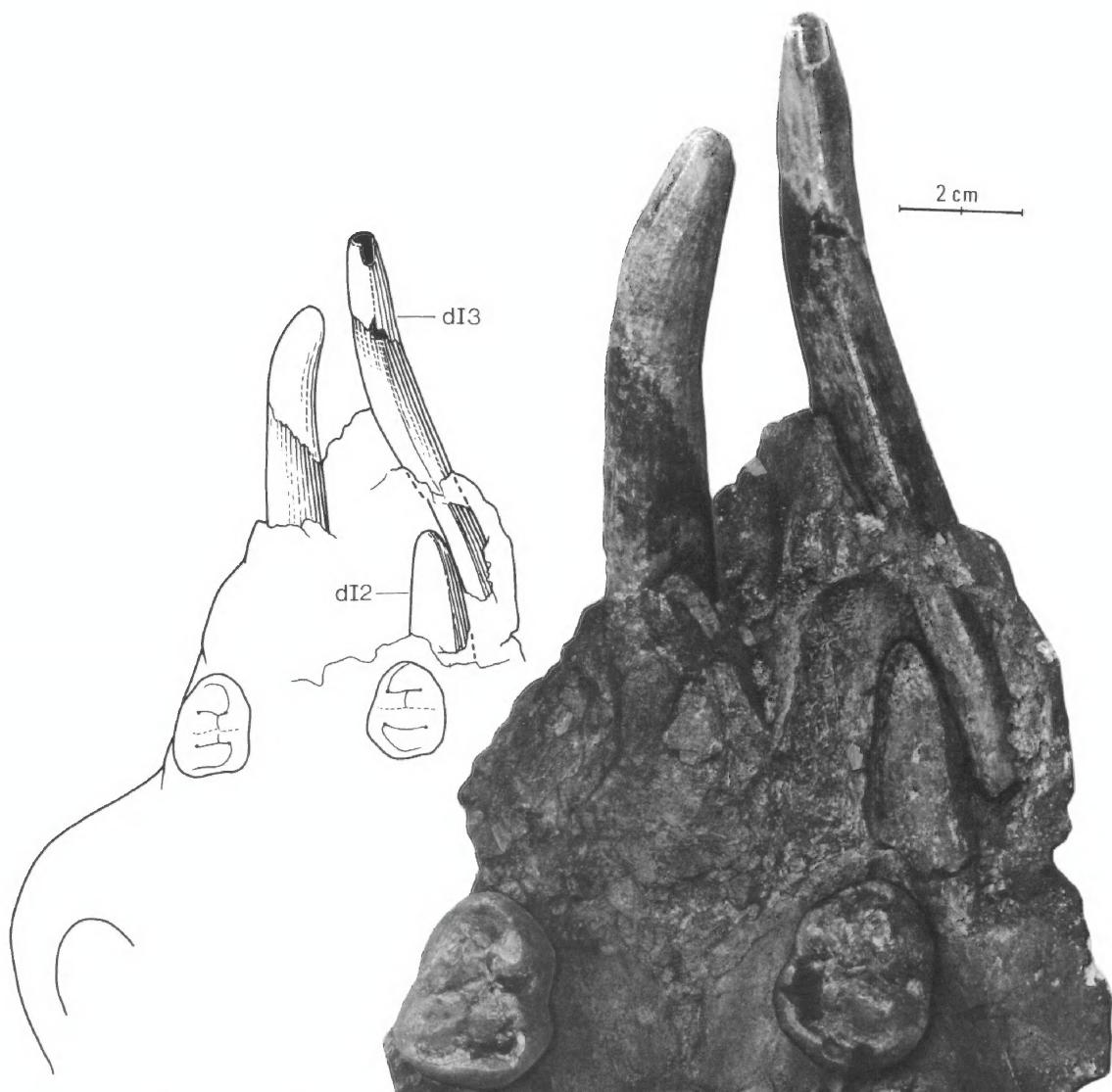


Fig. 3. *Amebelodon floridanus*, rostrum showing associated tusk germ (dI2) and transitory incisor (dI3) (skull with erupted DP2-3, F:AM 99415). Mixson's Bone Bed (Early Hemphillian), Florida.

has also already lost the lateral incisor. On this specimen one can see the more medial incisor at an early stage of growth with the formation of the enamel band beyond the enamel cap. Here, the developmental stage of the incisor (the permanent one) is intermediate between those described on F:AM 99415 and F:AM 99487.

Several isolated incisors, either transitory or permanent, had been found at Mixson. One juvenile tusk (F:AM 99416; fig. 4) has a rather long enamel cap which is followed lat-

erally by an enamel band. Measurements of F:AM 99416 are: length 164 mm; transverse section taken at 95 mm from the tip  $31.8 \times 23.4$  mm.

One transitory incisor (F:AM 105200; fig. 5) shows an enamel cap lengthened ventro-laterally, but neatly separated from the root by a distinct cervix, which bears a ventral ridge and enamel buds at the tip. Cement covers the rest of the incisor. These characters are present on each observed transitory incisor from the Frick Collection; the pres-

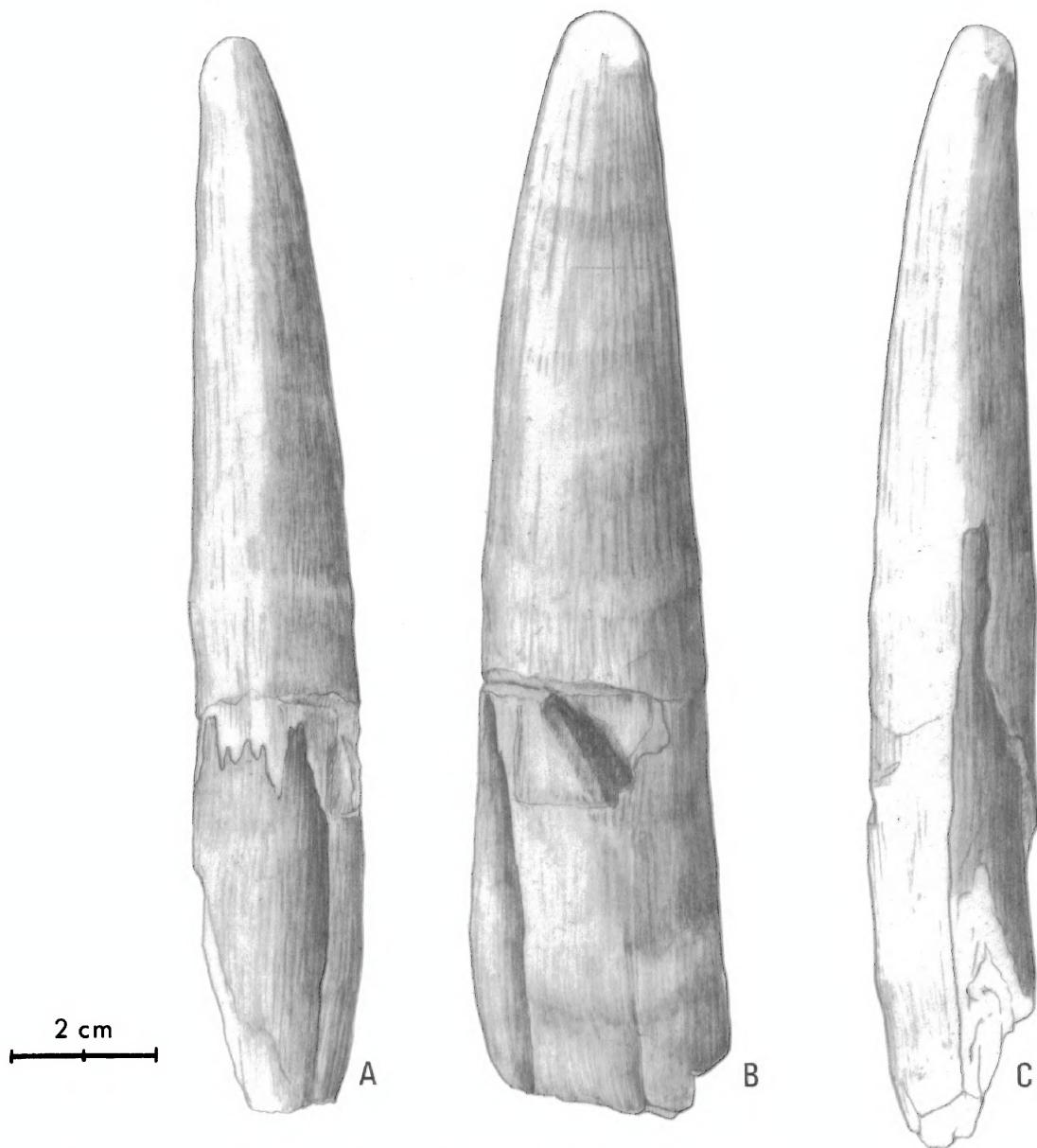


Fig. 4. *Amebelodon floridanus*, right di2 (F:AM 99416). A, dorsal, B, lateral, C, ventral. Mixson's Bone Bed (Early Hemphillian), Florida.

ence of a cervix, a true root with a rather flattened transverse section, and the lack of a lateral expansion (enamel band) are characters that can be used to distinguish upper transitory incisors from juvenile permanent upper tusks. Measurements of F:AM 105200 are: length 91 mm; minimal (dorsal) length of the enamel cap 26 mm; maximal (lateral) length of the enamel cap 41 mm; transverse

section taken at 70 mm from the tip 18.7 × 12.3 mm.

The total lifespan of the lateral incisor (transitory incisor) is very short (dental ages I and II), with some variation inside the time range since one specimen of dental age II has already lost the lateral incisor. The eruption of the medial incisor can be seen at dental ages II or III. At any rate, the eruption of the

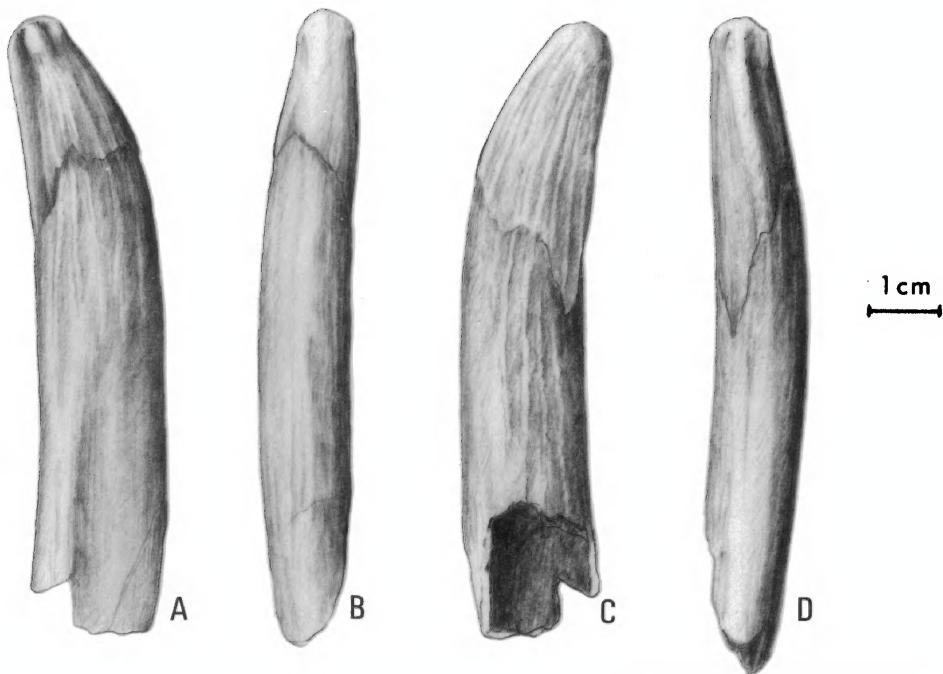


Fig. 5. *Amebelodon floridanus*, right di3 (F:AM 105200). A, medial, B, dorsal, C, lateral, D, ventral. Mixson's Bone Bed (Early Hemphillian), Florida.

permanent tusk is very precocious and fits with what is known among both trilophodont and tetralophodont gomphotheres.

#### LOWER INCISORS

Though living elephants lack lower incisors, the occurrence of lower tusks is well known among fossil elephantoids. Moreover, the association in a mandible of the two incisors (transitory incisor and tusk) had been already observed by Peterson (1926: 275, pls. 22, 23; see also Frick, 1926: 134; 1933: 632, figs. 2, 3) in the mammutid species *Mammut americanum* from Frankstown (Pennsylvania) and by Osborn and Granger (1932: 5–6, figs. 2, 3) in the amebelodontid species *Platybelodon grangeri* from the Middle Miocene of China (Tung Gur Formation, Inner Mongolia).

The mammutid specimen is a complete immature mandible with erupted Dp2–Dp3 at an early stage of wear and erupting Dp4. It has two pairs of incisors, both protruding out of the symphysis. The nature of these incisors had not been clearly explained by

Peterson. The larger incisors have “no enamel” (Peterson, 1926: 275). The other pair, upper and somewhat more laterally situated than the larger pair, are shorter with a tip of “three connected portions” (Peterson, op. cit.) and probably three apical enamel buds. Frick (1926: 134) compared these incisors to the so-called upper deciduous and permanent tusks of the living elephant.

The specimen of *Platybelodon grangeri*, described as a fetus by Osborn and Granger (1932), is a complete mandible associated with a partial palate. On the mandible, Dp2 and Dp3 are erupting and Dp4, as a germ, is in formation. The symphyseal rostrum had been dissected on the left side and shows the two incisors. The biggest protrudes out of the dentary and the other is a germ situated mediiodorsally to the protruding incisor. Osborn and Granger (1932: 6, fig. 2C–D) interpreted both incisors as “di?” and emphasized that “the presence of two incisors, one lying directly above the other and less advanced in growth is a bit puzzling. It is presumed that the lower and more advanced one is a deciduous tooth.” Since Osborn and Granger’s

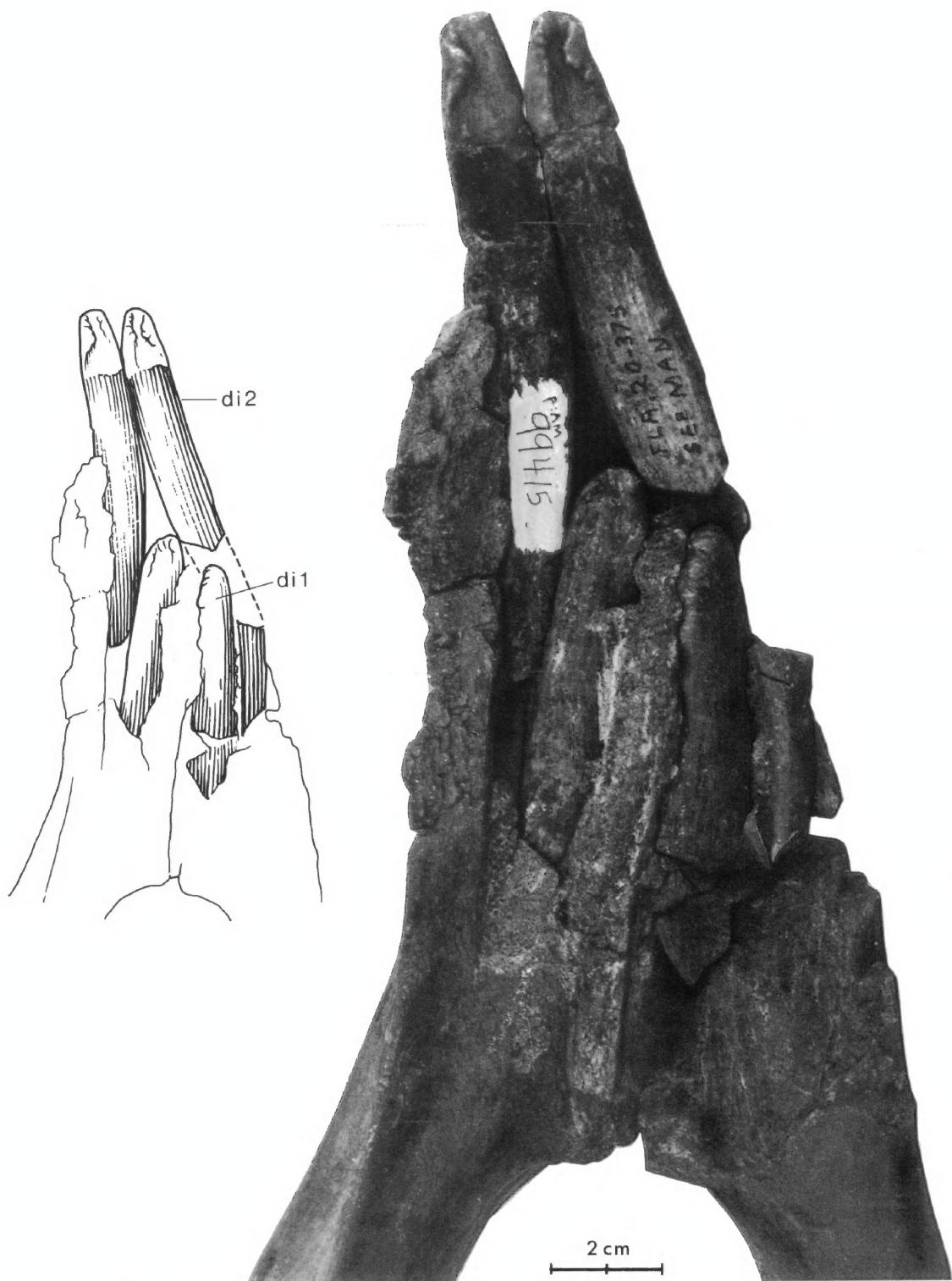


Fig. 6. *Amebelodon floridanus*, mandibular symphysis showing both tusk germs (di1) and transitory incisors (di2) associated (mandible with erupted Dp2–3, F:AM 99415). Same individual as fig. 3. Mixson's Bone Bed (Early Hemphillian), Florida.

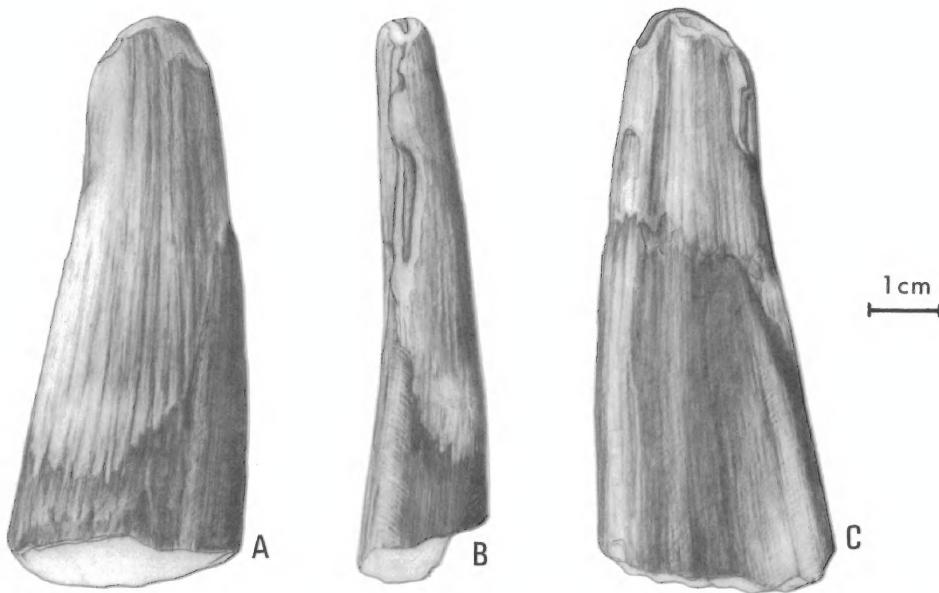


Fig. 7. *Amebelodon floridanus*, right di1 (F:AM 99523). A, ventral, B, lateral, C, dorsal. Mixson's Bone Bed (Early Hemphillian), Florida.

study, the lateral left incisor has been sectioned: the dentine is not tubular (no "rod cones"), contrary to the permanent lower tusks of that species. The tip of the lateral incisor is covered by an enamel cap with lateral buds forming a ridge. The germ of the medial incisor also possesses an anterolateral ridge made of enamel buds.

The sequence of lower incisor development can be deduced from the study of several juvenile mandibles of the species *Amebelodon floridanus*. These specimens show that the association of the two incisors observed by Osborn and Granger in *P. grangeri* is not "puzzling" and can be interpreted as for the upper incisors.

A mandible associated with the cranium previously described (F:AM 99415; fig. 6) shows the association of both tusk and tusk. The lateral incisor protrudes out of the dentary and a germ is situated dorsomedially. An enamel cap covers the tip and is well separated from the root by a very distinct cervix. The enamel cap is short and has a medial bud and a thick lateral budded ridge. On the contrary, the medial germ is entirely covered by a layer of enamel with dorsolateral buds forming a ridge. This germ is more robust than the lateral incisor. Measurements of

F:AM 99415 are: visible length of the lower right lateral (transitory) incisor 91 mm; transverse section  $18.4 \times 12.2$  mm; ventral length of the enamel cap 35 mm; transverse section of the medial incisor (tusk)  $28 \times 15.5$  mm.

Another mandible associated with the cranium previously described (F:AM 99454) has lost its pair of lateral incisors. The right permanent tusk protrudes out of the rostrum. As for the germ seen on F:AM 99415 (fig. 6), its tip is covered by an enamel cap longer than that of the transitory incisor, with a dorsolateral ridge made of buds, and without any cervix. The smaller size of the tusk compared to that of F:AM 99415 can be due to individual variation and different timing of the growth of the incisor. Measurement of F:AM 99454 is: transverse section of right lower tusk  $21.6 \times 10$  mm.

Comparison of numerous isolated tusks and tusks shows that juvenile tusks (F:AM 99523; fig. 7) never have a cervix which separates the enamel cap from the rest of the incisor: there is no real root. As the tusk grows, the enamel cap is worn, first on the anterolateral border (where the ridge is), then the dorsal face, and finally the ventral face. Measurements of F:AM 99523 are: length of specimen (broken) 82.5 mm; transverse sec-

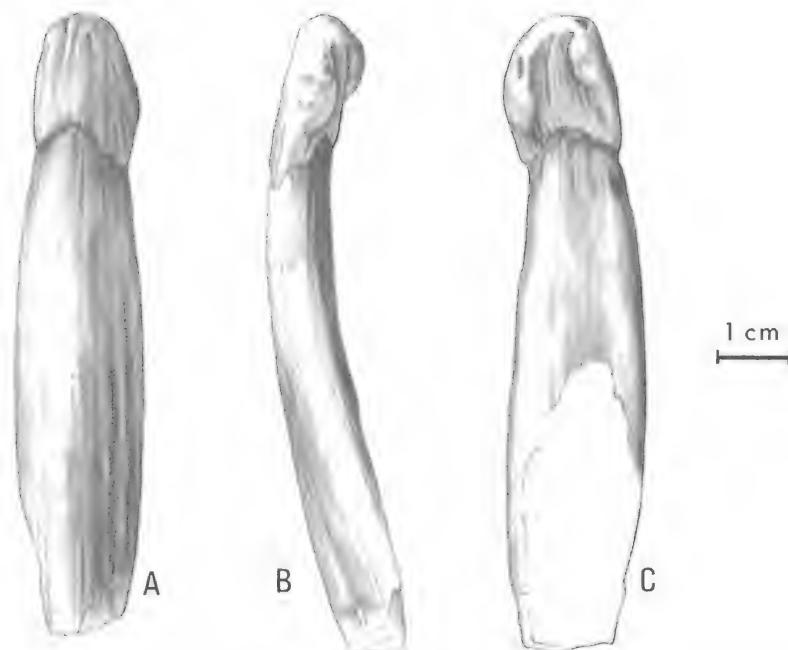


Fig. 8. *Amebelodon floridanus*, left di2 (F:AM 99586). A, ventral, B, lateral, C, dorsal. Mixson's Bone Bed (Early Hemphillian), Florida.

tion at the fracture  $34 \times 13.4$  mm; medial length of enamel cap 29.5 mm; ventral length of enamel cap 67.3 mm.

On a more mature tusk (F:AM 99522) with a transverse section of  $43 \times 18$  mm, the enamel has been entirely worn.

On the lower transitory incisors (F:AM 99586; fig. 8), the enamel cap is always well separated from the root by a cervix. Wear occurs on the anterior border and dorsal apex. The pulp cavity is closed at the origin of the tooth. Measurements of F:AM 99586 are: length 89.2 mm; transverse section taken at 55 mm from the tip  $19.6 \times 9.8$  mm; maximal (ventrolateral) length of the enamel cap 24 mm.

As for the upper incisors, the total lifespan of the lower transitory incisors is extremely short and the permanent lower tusks precociously erupt when DP2 and Dp3 become functional.

Based on the sequence of tooth eruption seen in *Amebelodon floridanus*, one can argue that in the mandible of *Platybelodon grangeri* described by Osborn and Granger (1932), the lateral incisor is the transitory one and the medial is the permanent tusk. In the man-

dible of *Mammut americanum* described by Peterson (1926), the upper and somewhat more medial incisors with enamel buds at the tip are the erupting permanent tusks and the lower and longer incisors with no enamel (lack probably due to wear) are the tusks soon to be shed.

#### ISOLATED TRANSITORY INCISORS AND TUSKS OF EUROPEAN ELEPHANTOIDS

Isolated juvenile incisors of other elephantoid taxa can be interpreted safely by comparisons with *Amebelodon floridanus*, assuming that the interpretations for *A. floridanus* are correct. The upper transitory incisor of *Gomphotherium angustidens* (CV 1002; fig. 9) shows no difference with *Amebelodon floridanus*, except its smaller size and straight (not concave) lateral face. The lower transitory incisor (CV 1003; fig. 10) is more concave dorsally (a specific character also observed on the mature lower tusks). Though the tip of the incisor seen in figure 10 is worn, the enamel cap appears to be smaller and more delicate with smaller buds than in *A. floridanus*. The wear facet is situated at the

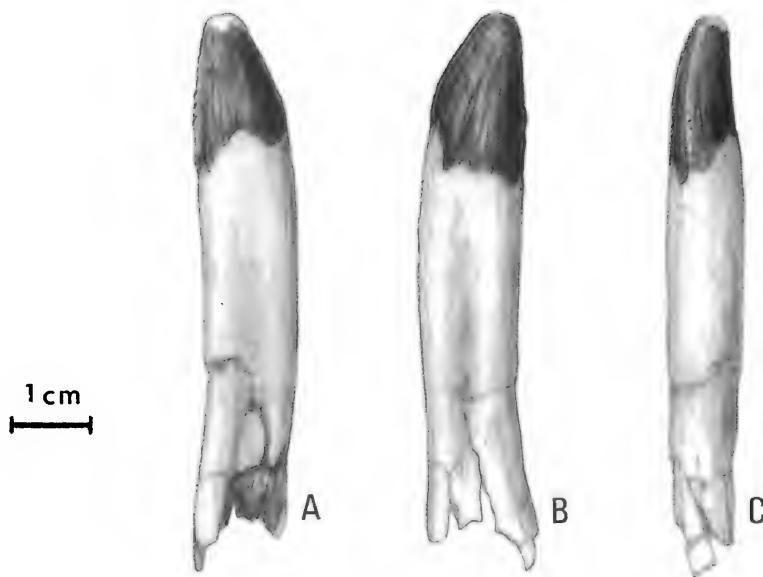


Fig. 9. *Gomphotherium angustidens*, right di3 (CV 1002). A, medial, B, lateral, C, ventral. Castelnau-Barbarens (Astaracian), Gers, France.

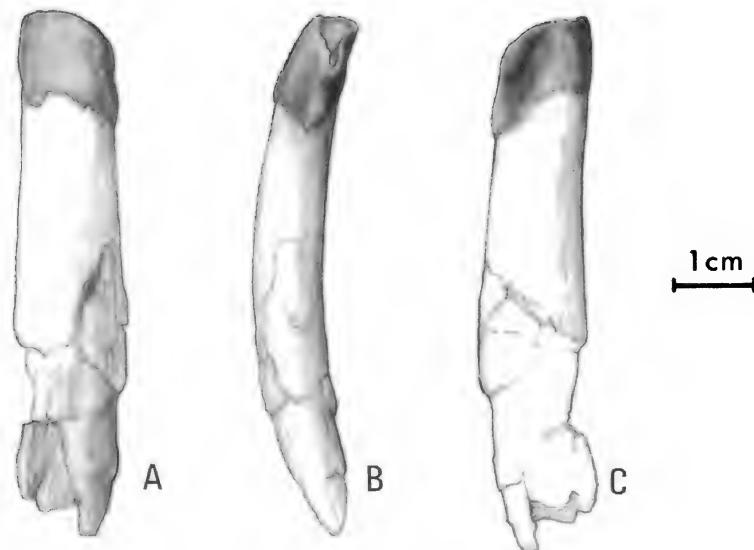


Fig. 10. *Gomphotherium angustidens*, left di2 (CV 1003). A, ventral, B, lateral, C, dorsal. Castelnau-Barbarens (Astaracian), Gers, France.

tip anteriorly and cuts the enamel. Length of CV 1002 (upper transitory incisor fractured specimen) is 73.6 mm and the maximal (ventral) length of the enamel cap is 23.2 mm. Measurements of CV 1003 (lower transitory incisor) are: length 68 mm; lateral length of the enamel cap (worn) 15.2 mm; transverse

section taken at 38 mm from the tip 14 × 8.9 mm.

A lower transitory incisor of *Gomphotherium* sp. from the Loire Basin (Ba 1794, fig. 11) belonged to an older individual than CV 1003. The enamel cap is more worn but the cervix is still apparent. There is no pulp cav-

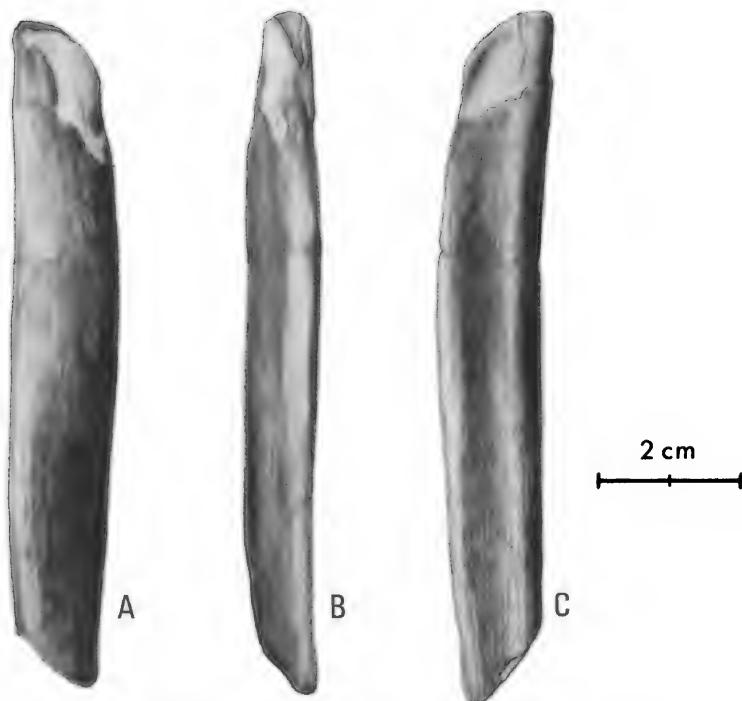


Fig. 11. *Gomphotherium* sp., left di2 (Ba 1794, MNHN). A, ventral, B, lateral, C, dorsal. Baigneaux (Orleanian), Loiret, France.

ity. As for *G. angustidens*, the main wear facet is anteriorly situated at the tip and cuts the enamel. In contrast to *G. angustidens* the incisor is not curved. Measurements of Ba 1794 (MNHN) (lower transitory incisor) are: length 98.4 mm; transverse section taken at 38 mm from the tip  $15.5 \times 9$  mm; ventral length of the enamel cap 22 mm.

A more worn lower transitory incisor (CV 1001; fig. 12) shows no trace of enamel. A smoother anterodorsal wear facet cuts the cement. Though the morphology of the enamel cap cannot be seen, this tooth can be interpreted as a transitory incisor because the root is closed: no pulp cavity is seen at the narrowing transverse section close to the origin of the tooth. Measurements of CV 1001 (lower transitory incisor) are: length 54 mm; transverse section taken at 38 mm from the tip  $15 \times 8.2$  mm.

When the enamel is completely worn out it is difficult to distinguish small juvenile permanent incisors from worn transitory incisors as shown in figure 12. Two tips of incisors of *Gomphotherium angustidens* (SEP

212, SEP 219, figs. 13, 14) from En Péjouan (Astaracian) with no enamel show only dorsolateral and ventral wear facets which cut the cement, like more mature tusks of the same species. There is also a small medial facet due to the contact with the symmetrical

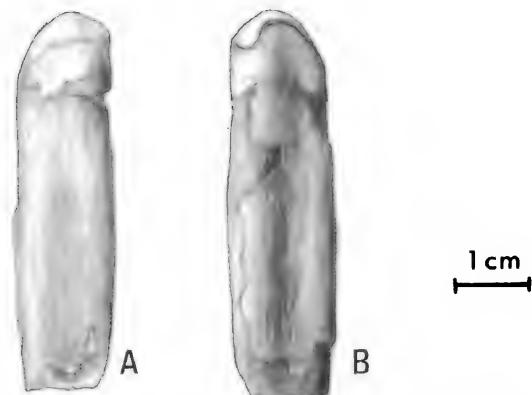


Fig. 12. *Gomphotherium* sp., right di2 (CV 1001). A, ventral, B, dorsal. Crastes (Orleanian), Gers, France.

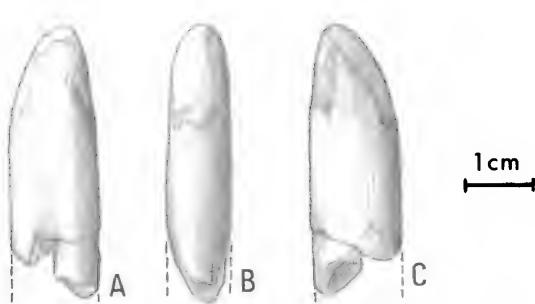


Fig. 13. *Gomphotherium angustidens*, right di1 (SEP 219, MNHN). A, ventral, B, lateral, C, dorsal. En Péjouan (Astaracian), Gers, France.

incisor. The pattern of those facets suggests that these juvenile incisors are permanent tusks. Length of SEP 212 (MNHN) (lower tusk) (fractured specimen) is 30.8 mm. Measurements of SEP 219 (MNHN) (lower tusk) are: length (fractured specimen) 41.5 mm; transverse section at the fracture 14.4 × 8.3 mm.

Lower tusks of young specimens which belong to the primitive amebelodontid species *Archaeobelodon filholi* (see Tassy, 1984: 462; 1985: 568, for description of this species), are contemporaneous with but wider and flatter than those of *G. angustidens* and fairly common in the Astaracian locality of Sansan. They recall those of *Amebelodon floridanus*. The most juvenile specimen known (Sa 9314; fig. 15) has an enamel cap with no cervix. Lateral buds form a ridge. As for more mature tusks of *Archaeobelodon filholi*, this juvenile tusk is less enlarged than the tusks of *Amebelodon floridanus*. By its size, proportions, and morphology this specimen recalls juvenile tusks of *Platybelodon danoyi* from Belometcheskaya described as "id<sub>2</sub>" by Belyaeva and Gabunia (1960: 89, fig. 12; "*Platybelodon jamandzhalgensis*"). A small narrower isolated lower incisor described by Tobien (1973: 259, pl. 26, fig. 24) in the same locality as the specimen Sa 9314, could be a tusk of *A. filholi* though the cervix is not clearly marked. Measurements of Sa 9314 (MNHN) (lower tusk) are: length (fractured specimen) 54 mm; transverse section taken at 38 mm from the tip 24 × 13.2 mm; ventrolateral (maximal) length of the enamel cap 44.8 mm; medial (minimal) length of the enamel cap 19.4 mm.

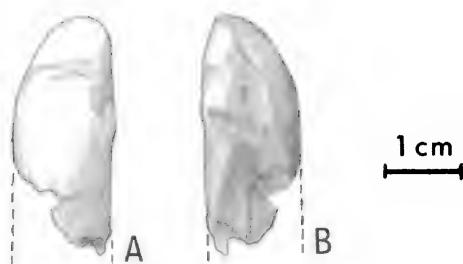


Fig. 14. *Gomphotherium angustidens*, right di1 (SEP 212, MNHN). A, ventral, B, dorsal. En Péjouan (Astaracian), Gers, France.

#### DECIDUOUS NATURE AND NUMBERS OF ELEPHANTOID TRANSITORY AND PERMANENT INCISORS

The interpretation of the nature of the two associated incisors observed on the cranium and mandible in elephantoids is somewhat tentative since we know only their postnatal development. Nevertheless, two hypotheses can be drawn.

On the one hand, one can interpret the two incisors as belonging to two successive dentitions, an hypothesis rejected here. On the other hand, one can interpret the two incisors as being elements of the primary dentition; in other words, as deciduous incisors never replaced.

#### HYPOTHESIS OF DENTAL REPLACEMENT

Because of the position of the two successional tooth buds in prenatal development stages (Anthony, 1933: 114; Moss-Salentijn, 1978: 24), in mammals, the germ of a replacement incisor is generally not just behind the milk tooth but close to its root, situated medially and deeper. Consequently, the respective positions of the two upper and lower incisors can be interpreted as proof of dental replacement of a lateral milk tooth by a medial definitive tooth. In this case the incisors could be either (\* indicates the permanent tusk):

di1/i1–I1\*/i1\* or  
di2/i2–I2\*/i2\* or  
di3/i3–I3\*/i3\*

Only the second solution supports the homology between the elephantoid tusk and the

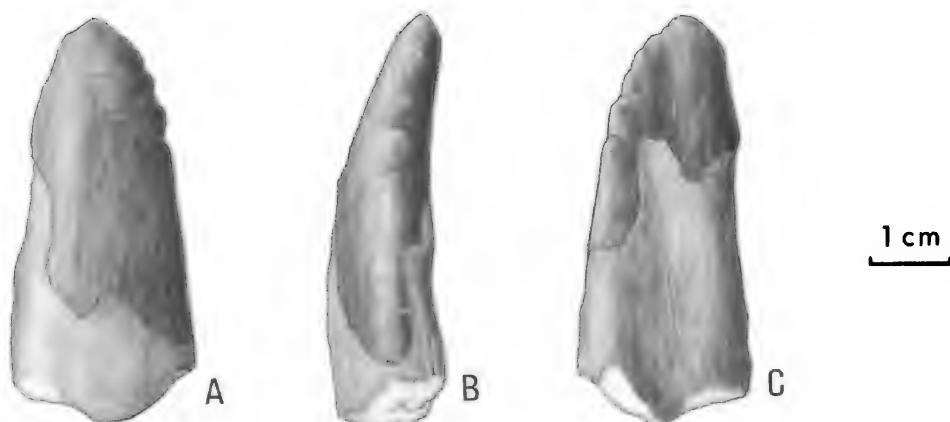


Fig. 15. *Archaeobelodon filholi*, left di1 (Sa 9314, MNHN). A, ventral, B, lateral, C, dorsal. Sansan (Astaracian), Gers, France.

inflated second incisor of *Moeritherium*. If this homology is accepted, one must admit a total reversion in the sequence of eruption of permanent incisors: late in the genus *Moeritherium* (with or just before M3), and very early among elephantoids (before DP4). The precocity of the eruption of the permanent tusk possibly falsifies the hypothesis of dental replacement. Indeed the development of the permanent elephantoid tusk is coincident with that of DP4 (the tusk even erupts before DP4, when no jugal tooth of the second dentition is in formation). This condition in amebelodontids and gomphotheres is not strictly a derived character for Neogene elephantoids, but is a much older evolutionary innovation. The holotype of *Phiomia serridens* from the Oligocene Fayum (Andrews, 1906: pl. 18, fig. 4) is half a mandible which shows an erupted tusk associated to a slightly worn Dp3 as in the specimen F:AM 99454 of *Amebelodon floridanus*. This tusk already displays the enamel buds which form the ridge seen on the Neogene Elephantoidea, with no cervix. It too matches closely with a more mature tusk of *Phiomia serridens*, a mandible with functional Dp3 and Dp4 and germ of m1 in formation, already described by Andrews (1908: 400, pl. 32, fig. 1).

Some cases are known where resorption of deciduous teeth occurs during prenatal stage with an early eruption of replacement teeth (I2 and P2 of *Tarsius*; see Luckett and Maier, 1982). Nevertheless, those cases are uncom-

mon and probably do not apply to elephantoids. One can also agree with Anthony (1933: 120) that, with respect to elephants, the characteristic trend of jugal teeth is the evolution toward the loss of replacement teeth, so that, by analogy, incisors can be held also as teeth of the first dentition.

#### HYPOTHESIS OF BOTH INCISORS AS DECIDUOUS TEETH

The preceding considerations lead to the hypothesis that both incisors, the lateral transitory incisor and the medial permanent incisor, are deciduous incisors which succeed rapidly without a true dental replacement. Nothing in the respective positions of the incisors contradicts this hypothesis. This hypothesis could also better explain the fact that both incisors can protrude together out of the symphysis during a short period of time, an uncommon feature for homologous deciduous and permanent teeth (see the mandible of *Mammut americanum* described by Peterson, 1926: 275, pls. 22, 23; in this case the respective positions of the two pairs of lower incisors, more upper and lower than medial and lateral in the symphysis, could be due to the shortening and narrowing of the symphysis of brevirostrine shape).

That such big elephantoid hypsodont tusks are milk teeth is not surprising. Moss-Salentijn (1978) has shown that among rodents and lagomorphs, the hypsodont incisors be-

long to the first dentition and were never replaced. Thus, an hypertrophic incisor can be a milk tooth.

If the deciduous nature of both incisors is assumed, one must reject the hypothesis of homology between elephantoid tusks and the inflated I2/i2 of *Moeritherium*, a hypothesis of homology that was somewhat already weakened by the implied reversion in the timing of eruption of permanent incisors. One must also recall that the elephantoid tusk is medial to the tush and that in *Moeritherium*, which had already lost one lower incisor (i3), the inflated lower incisor is lateral to the smaller one.

Following the hypothesis of the deciduous nature of the incisors, the position could be the following (\* specifies the permanent tusk):

dI1\*/i1\*-dI2/i2 or  
dI2\*/i2\*-dI3/i3

It is not ascertained that both upper and lower incisors belong to the same loci. On the contrary, on the basis of the lateral position in the premaxilla of the upper transitory incisor and of the medial position (close to the symphyseal sutural plane) of the lower transitory incisor, one can assume the loss of the first upper locus and of the third lower locus. In this case, the homology of the loss of dI3/i3 locus in *Moeritherium* and in Elephantoidea can be assumed. The interpretation of the elephantoid incisors would be:

upper incisors: dI2\*-dI3  
lower incisors: dI1\*-dI2

Anthony's (1933) interpretation (followed by Tassy et al., 1977) that the upper tusk in elephantoids is the third incisor, must be rejected, because of the position of the permanent incisor medial to the transitory one. Anthony's (1933: 97) hypothesis relied on the observation of a fetus of *Elephas maximus* of a diverticulum derived from the alveolus of the transitory incisor (diverticulum interpreted as the first locus). The transitory incisor would then be the second one and the permanent incisor the third: the dI3 would have migrated secondarily medial to dI2. This is rather unlikely and there is no other evidence that this diverticulum is homologous with the first locus. The hypothesis identi-

fying both tusks as dI2 and dI1 requires less ad hoc explanations.

In conclusion, the hypothesis proposed here for the two pairs of upper and lower incisors (dI2\*-dI3/dI1\*-dI2) for the elephantoids is based on:

- (1) the precocity of incisor development and succession,
- (2) the observed association of the two pairs of lower incisors protruding out of the symphysis during a short period of time,
- (3) the position of the loci in the premaxilla and the mandibular symphyseal rostrum,
- (4) the hypothesis of homology of the loci between *Moeritherium* and elephantoids, and
- (5) the analogy with rodents and lagomorphs, in which hypsodont incisors are deciduous teeth.

## CONCLUSIONS

The paleontological data provide some evidence that the elephantoid tusks are dI2 and dI1, but this evidence is less than decisive. The analysis of recent material (possible for upper incisors) will confirm or refute the present hypothesis. One must agree with Moss-Salentijn (1978) and Luckett and Maier (1982) that the best criterion to identify the deciduous or replacement nature of teeth is the identification at prenatal stages of the embryological relations between the enamel organ of the teeth of the primary and secondary dentition. The enamel organ of the replacement tooth derives from the external epithelium of the enamel organ of the corresponding deciduous tooth, on the medial side. The identification of this derivation or its absence is crucial to the problem. Anthony (1933: 73, 86, pl. 1, figs. 11, 12) described developing permanent incisors ("incisive définitive") in two fetuses of *Elephas maximus* (length unknown) and *Loxodonta africana* (length from the trunk to the tail: 760 mm). No epithelial layer is described between the two upper incisors. This observation supports the hypothesis chosen here, but more studies on younger specimens are necessary to settle the issue.

If the hypothesis favored here is correct, the independent development of tusks in *Moeritherium* and in Elephantoidea must be

assumed. Only the locus of the second upper incisor would be homologous for both taxa, but not the tusk itself. This result should not be surprising since other kinds of tusks appeared independently among other *Tethytheria*, for example, in dugongs and in desmostylians.

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